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NEW LIGHT ON BLENDING AND MENDELIAN INHERITANCE

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THE question whether blending or intermediate inheritance involves Mendelian principles is of prime interest to every student of genetics. The further question whether Mendelian characters are constant or variable is not less important. New light is shed on both these questions by a recent and valuable investigation by Y. Hoshino, "On the Inheritance of the Flowering Time in Peas and Rice."

The investigation is to be most highly commended for its thoroughness. It has involved the raising of over 30,000 plants extending over a period of 8 years. F_2 and F_3 generations have been raised three times and F_4 twice. The publication contains a careful summary and analysis of the facts observed. Above all it contains *facts* with a minimum of speculation, not facts so marshalled as to prove a particular theory and otherwise useless, but facts which the reader may study from any angle he chooses. I propose to exercise the privilege which our author's commendable method of publication makes possible, of utilizing his facts for testing a slightly different theoretical interpretation from that which he adopts, for I am acquainted with no material equally valuable in relation to the two questions stated above, though I have been engaged for many years in studying these same questions.

Hoshino crossed two varieties of peas which differed in flowering time by about three weeks. The early variety was white-flowered, the late variety red-flowered. The F_1 hybrids were only a little earlier than the late variety in time of flowering and of course had red flowers, this being a dominant character. The F_2 hybrids varied in time of flowering throughout the range of both parent varieties and all intermediate points, but not beyond the range of the parents. Hoshino divides the F_2 plants into two main groups, an early flowering and a late flowering group, the two being separated naturally by a class of "minimal frequency" usually recognizable. A majority of the plants in the early flowering group had white flowers, a majority in the late flowering group had red flowers. This result shows that early and late flowering have a tendency to segregate from each other as Mendelian allelomorphs and that time of flowering is *coupled* with flower color. This fact of coupling, first observed by Lock, alone would suffice to show that time of flowering is inherited as a Mendelian character. The fact that the F_2 individuals apparently fall into two main groups, not into four or eight, indicates that one important Mendelian factor is concerned, not two or three. But Hoshino found that in F_3 four (not two) groups of relative constancy were obtained and this has led him to suppose that the inheritance of time of flowering depends upon *two* independent Mendelian factors, one of which (A, a) determines late or early flowering, while the second (B, b) supplements or modifies the action of A. He regards A as the *principal* factor, with which alone flower color shows coupling. The action of B is regarded as subsidiary. A characterizes late-flowering plants; a, early-flowering plants. B makes the flowering time later than it would be otherwise; b of course makes it earlier. The four supposedly homozygous sorts which are recognized are of the following formulæ:

aabb, early; aaBB, intermediate early; AAbb, intermediate late; AABB, late. Since red color of flowers is by hypothesis coupled with A, red flowers will predominate in the last two groups, white flowers in the first two as observed, and the dividing line between them will correspond with Hoshino's class of minimal frequency in F_2. But the plants which Hoshino classified, on the basis of F_3 and F_4 tests, as extracted early (aabb) and extracted late (AABB) are usually not quite so early or late, respectively, as the uncrossed races. Hence he assumes the occurrence of "gametic contamination," and recognizes classes of "would be" or "pseudo"-early and "pseudo"-late. He also notes the occurrence of "qualitative" variation within the groups classed as "constant" early intermediate and "constant" late intermediate. That is one family supposed to be of the same genetic formula as another may throughout its entire range produce plants slightly *earlier* or *later* than those of the other family. This behavior is not ascribed to any difference in genetic formula, but to a slightly different value of the same gene in the two families.

The late race employed was also found to vary in lateness, one "pure line" derived from it being later than another. Crosses made with these two lines are reported separately. No factorial difference is recognized between them. Each is AABB, but one flowers a little later than the other and transmits this property to its descendants. Thus "qualitative" variation of a gene, *i. e.,* variation in its potency, is recognized by Hoshino. Aside from the occurrence of two pure lines in the late race, Hoshino considers "the flowering time quite fixed and unchangeable in the parent varieties," and cites his Tables IV–VI in support of this idea. Table VI is of particular interest in this connection because in this case seeds were planted of the earliest flowering and latest flowering individuals of the same pure line and descended from the *same individual grandparent.* These plantings constitute a test of the existence of genetic variation within the pure line. The progenies of the same grandparent plant (but of different parents) are so obviously alike and so little variable in flowering time that Hoshino has not considered it necessary to calculate their mean flowering time. But if this is done it affords unmistakable evidence that genetic variation occurs within these "pure lines" (see Table I). For in all but the last two of the thirteen cases tested the earlier parent has the earlier progeny. From long experience in studies of rats with such small differences as are here indicated I have no hesitation in concluding that fluctuating variation of genetic significance is here in evidence.

To recapitulate, as regards genetic variation in flowering time, Hoshino (1) recognizes that gametic contamination results from crossing early and late flowering varieties; (2) recognizes also that variation may occur among the cross-bred families, as well as in different pure lines of the uncrossed races, as regards the "quality," value, or potency of the same gene. (3) Although Hoshino does not refer to the fact, his observations show clearly that genetic variation of a graded or fluctuating sort occurs in at least one of the varieties which he crossed. It is probable that those varieties were as pure as are obtainable, but almost certain that their flowering time fluctuates slightly from genetic causes.

What I want to suggest is that in these several agencies we have a sufficient explanation of the variations observed in Hoshino's F_2, F_3, and F_4 generations, without invoking a two-factor hypothesis, one factor being enough. Hoshino has shown that a three-factor, or multi-factor hypothesis will not fit the facts observed. Will not *one* factor fit them quite as well as two, provided gametic contamination occurs, which he admits? The "pseudo-early" and "pseudo-late" classes Hoshino explains plausibly as due to gametic contamination. Could not the "intermediate early" and "intermediate late" be reasonbly explained as due to *further* contamination? For they intergrade with the pseudo-early and pseudo-late classes, respectively, and also with each other. From Hoshino's carefully controlled results, it is perfectly clear that early and late flowering are allelomorphs, and that segregation of early and late types occurs in F_2 but attended by gametic contamination. It is perfectly clear that the contamination is not uniform in amount. Sometimes little or no contamination is observable; sometimes it is considerable.

TABLE I

COMPARISON OF THE MEANS OF FAMILIES DESCENDED FROM THE SAME PURE-LINE GRANDPARENT, BUT FROM PARENTS OF UNLIKE CHARACTER

Based on Hoshino's Table 6.

Designation of Grandparent	Mean, Progeny of Earlier Parent	Mean, Progeny of Later Parent	Difference
Gp. I.4	59.96	60.11	.15
Gp. XVI.3	59.94	60.65	.71
Gp. XII.8	60.16	60.50	.34
Gp. VIII.3	63.65	63.98	.33
Gp. VIII.4	63.86	64.21	.35
C.12	60.25	60.58	.33
C. 65	59.43	60.05	.62
C. 61	62.91	64.18	1.27
C. 88	64.23	64.56	.33
Gp. XVI.3.5	66.45	66.63	.18
C. 65.27	66.22	67.30	1.08
Gp. VIII.4.23	71.75	71.20	–.55
C. 61.21	72.00	71.25	–.75

Contamination sufficiently great would account for the intermediate early as a *modified* early class and the intermediate late as a *modified* late class. The matter of coupling is unaffected by this hypothesis, since coupling is shown with only *one* factor, Hoshino's factor A. The observed variability and intergradation of the two intermediate classes favors a hypothesis of contamination rather than one of an independent modifying factor.

If we suppose modification due to gametic contamination to occur in half of the gametes formed by F_1 individuals and that this contamination is definite in amount (say equivalent to 5 days) the F_2 expectation would be exactly the same as from a two-factor system such as Hoshino adopts. As a matter of fact neither supposition is exactly correct. If we adopt contamination as a sufficient explanatory hypothesis, we must suppose the amount of contamination to be variable; if we adopt a definite modifying factor, we must suppose the amount of modification to be variable.

To make the matter clear, let us suppose the early race to be stable at 35 days between sprouting and flowering and the late race to be stable at 55 days. According to Hoshino's hypothesis aabb stands for a 35-day period, and AABB for a 55-day period. If we assign to the assumed modifying factor B a delaying effect of five days, then the class aaBB (early intermediate) will have a value of 40 days, and the other homozygous class AAbb (late intermediate) will have a value of 50 days. Heterozygous classes will be intermediate as follows:

TABLE II

COMPOSITION OF F_2 ON HOSHINO'S TWO-FACTOR HYPOTHESIS, WITH EQUIVALENTS IN DAYS FROM SPROUTING TO FLOWERING

Designation and Expected Frequency	Homozygous	Heterozygous	
		Monohybrid	Dihybrid
1 aabb	35		
2 aaBb		37.5	
1 aaBB	40		
2 Aabb		42.5	
4 AaBb			45
2 AaBB		47.5	
1 AAbb	50		
2 AABb		52.5	
1 AABB	55		

If, however, we replace the modifying factor B in this scheme by a modification in A amounting to 5 days, then we can dispense with B and yet obtain exactly the same classes and in the same numerical proportions and with nearly the same expectations as regards their breeding capacity. Let us assume that a stands for a 35-day period, A for a 55-day period, and that modified a, which we will call a′, stands for a 40-day period, and modified A, which we will call A′, stands for a 50-day period and that all are allelomorphs of each other. Then the F_1 gametes will be a + a′ + A′ + A and F_2 will contain the classes shown in Table III.

It is evident that both schemes fit the observed facts fairly well. Either one will explain the decreased variability of F_3 as compared with F_2 and the production of several different types of F_3 families differing in the amount of their variability, some of which are relatively constant. But the former scheme will not answer without the further assumption of gametic contamination (which Hoshino makes) and the latter must invoke contamination of different degrees in order to explain the pseudo-early and pseudo-late classes. The former scheme involves two explanatory principles, the latter only one. Other things being equal, the simpler hypothesis is to be preferred.

TABLE III

COMPOSITION OF F_2 ON A ONE-FACTOR HYPOTHESIS WITH CONTAMINATION OF A DEFINITE AMOUNT (5 DAYS) IN HALF THE GAMETES

Designation and Frequency	Homozygous	Heterozygous, All Monohybrid			
		Difference, Conj. Gam., 5	Difference 10	Difference 15	Difference 20
1 aa.........	35				
2 aa′........		37.5 (35:40)			
1 a′a′........	40				
2 aA′........				42.5 (35:50)	
2 aA.........					45 (35:55)
2 a′A′.......			45 (40:50)		
2 a′A........				47.5 (40:55)	
1 A′A′......	50				
2 A′A.......		52.5 (50:55)			
1 AA........	55				

Experiments decisive between the two hypotheses are difficult to devise, but certain tests are possible. On the hypothesis of Hoshino one would not expect to obtain a class splitting into homozygous early intermediate and homozygous late intermediate. On the alternative hypothesis such a class (40–50) should be obtainable. *A "constant" class exactly intermediate between the parent varieties* (say 45) *would be impossible on Hoshino's hypothesis,* unless he is willing to admit an indefinite amount of contamination, which, however, would render the two-factor hypothesis superfluous. On the alternative hypothesis such a constant intermediate class should be obtainable after a sufficient number of inbred generations. In reality Hoshino's observations show that *it is obtained in F_4 and is then more abundant than any other "constant" class.* The largest group of hybrid offspring in Hoshino's experiments and that belonging to the latest inbred generation is his F_4 generation raised in 1914 (see his Tables G–U). This includes 231 families classed by Hoshino as "constant." They are descended from 15 different F_2 individuals ranging in flowering time (in 1912) from 48 to 65 days, this being practically the entire F_2 range. The combined range of the F_3 families raised in 1913 extended from 45 to 71 days. From certain individuals, selected at intervals throughout the ranges of the fifteen F_3 families so as to represent their complete variability seeds were planted which produced the F_4 generation. 421 such F_4 families were reared and studied and of these Hoshino regards 231 as "constant" because of the limited range of variation in flowering time of each. The others are regarded as still heterozygous. The mean flowering time of each of the "constant" families has been calculated by Hoshino and these means have the distribution shown in Table IV (omitting fractions from the class magnitudes which would make them .5 greater than those given in the table, but would not affect their distribution). It should be noted that on account of the peculiar weather conditions of 1914, the flowering time came about 10 days earlier than in the two previous years, the range of the F_4 means extending from 34 to 59 days, whereas the F_3 range of flowering time was from 45 to 71 days. Since both upper and lower limits of the range are displaced by like amounts and in the same direction, the general character of the distribution is not affected thereby.

TABLE IV

CLASSIFICATION OF MEANS OF F_4 "CONSTANT" FAMILIES FROM HOSHINO'S TABLES G–U

Classes	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
White..	1	13	5	2		3	18	12	15	14	13	12	3													
Red or mixed		2	1	1		1	2	1	4	13	17	6	6	2		5	3	3	2	11	16	3	10	8	1	1
Totals .	1	15	6	3		4	20	13	19	27	30	18	9	2		5	3	3	2	11	16	3	10	8	1	1

Table IV shows unmistakably that the F_4 constant families fall into three natural groups, not four as Hoshino's hypothesis would lead one to expect. The modes of these three groups fall at 35, 44 and 54, respectively, with frequencies of 15, 30 and 16, respectively. Each group is separated from the next adjacent by a gap (a class of 0 frequency). The modes of the early and late groups correspond closely with those of the uncrossed early and late parent varieties, which in this season had modes at 35 and 56, respectively. The third and largest group has its mode almost exactly midway between the modes of the early and late groups, with 8 intervening classes below it and 9 above. It would be difficult to imagine a finer example of a stable intermediate class produced by hybridization. For it will be remembered that every part of this population is stable, since it includes only families shown by Hoshino's breeding tests to be reasonably constant, those which he actually pronounced "constant." From it, therefore, one would need only to choose families of the desired flowering time, in order to have a complete succession of varieties from very early to very late.

But it may be asked, is the middle group possibly an "early intermediate" group of Hoshino's formula aaBB separated from the later groups by a class of minimal (0) frequency, as in the F_2 distribution? If so it should contain very few red-flowering families, no more indeed than the early group itself, since each would obtain red-flowered families only by cross-overs. Inspection of Table IV shows that this hypothesis is untenable. The truly hybrid origin of the middle group is shown by the large number of red-flowered or mixed families which it contains. Nine out of 12 of the F_3 families which contributed to the production of the middle group contained red-flowered or mixed red and white families. The middle F_4 group itself contained 90 white-flowered to 52 red-flowered or mixed families, whereas the early group contained 21 white: 4 red, and the late group contained only red-flowered or mixed families.

Hoshino observed that the flowering time of F_1 plants was close to that of the late parent, being only 2 or 3 days earlier, and considers this to be evidence of dominance, but I am inclined to think it should be interpreted differently, for F_2 plants having the genetic properties of F_1 plants are in some cases at least (Hoshino's Tables T and V) much earlier in flowering time, being in fact almost exactly intermediate between the parent races, although in one family (S) the F_2 plant was late like F_1, but its F_3 and F_4 descendants covered the entire range, as did those of T and U. I am inclined to interpret the inheritance as truly *intermediate* and to explain the lateness of F_1 and of an occasional F_2 individual as due to physiological non-genetic causes. Recent observations made on size inheritance in guinea-pigs together with certain observations recorded by Hoshino lead me to this conclusion. When the small *Cavia cutleri* is crossed with the relatively large guinea-pig, the F_1 hybrids are larger than either parent, but the F_2 hybrids as a group are close to intermediate and only a little more variable than F_1. A stimulus due to crossing makes F_1 larger than its genetic constitution would otherwise make it, but the added size due to this stimulus does not persist to any great extent beyond F_1. Hoshino's F_1 peas probably possess a similar vigor due to crossing, which quickly disappears in later inbred generations. If this vigor due to hybridizations causes extra growth it may delay flowering time, for Hoshino, confirming Keeble and Pellew, has shown that late-flowering plants have longer internodes than early-flowering ones.

Hoshino, as we have noted, divides his F_2 families into two portions, early-flowering (chiefly white) and late-flowering (chiefly red). But we have seen reason to think that the F_4 families fall naturally into three portions, early, medium and late, and it is possible to divide the F_2 families in a similar way, though of course somewhat arbitrarily, classing as early those falling within the range of the early parent or a little beyond it, and as late those which fall within the range of the late parent, while those which lie between are placed in the middle class. When the F_2 families are treated in this way we find the distribution of white-flowering and red-flowering plants shown in Table 5.

TABLE V

DISTRIBUTION OF WHITE- AND OF RED-FLOWERING AMONG THE F_2 PLANTS

Hoshino's Table	Early		Medium		Late		Total
	White	Red	White	Red	White	Red	
Table 2	49	13	20	114	7	168	371
Table 8, A_1	10	3	10	62	1	11	97
Table 8, A_2	17	2	2	20	3	25	69
Table 8, B_1	4	0	6	25	0	7	42
Table 8, B_2	17	0	7	37	5	30	96
Table 8, C	26	24	3	37	5	45	140
Total	123	42	48	295	21	286	815
Per cent. white	74		14		6.8		

Hoshino uses his F_2 tables as a basis for calculating the strength of the coupling between earliness and flower color, and concludes that the coupling is approximately 7:1. If, however, F_2 is divided as in Table 5, the coupling appears to be less strong, probably about as 4:1 or 5:1. The percentages of white-flowered plants expected in each group on various integral coupling ratios are as follows:

Coupling	Early Group	Medium Group	Late Group
4:1	64%	16 %	4 %
5:1	69%	14 %	2.8%
6:1	73%	12 %	2 %
7:1	76%	10.9%	1.5%
Observed	74%	14 %	6.8%

It will be observed that the percentage of white-flowered plants in the early group indicates about a 6:1 coupling ratio, but in the medium group, it indicates a 5:1 ratio, while in the late group it would indicate a 3:1 ratio. Much uncertainty exists as to the classification of many of the F_2 plants as regards flowering time, because of irregular and delayed germination. Undoubtedly the classes early, medium and late overlap, so that not much reliance can be placed on the categories adopted. But the figures given indicate that Hoshino has estimated too high the coupling strength, and that more probably it does not exceed 5:1. This is not due to any inaccuracy in Hoshino's calculations, but would follow only if the hypothesis suggested in this paper is substituted for Hoshino's hypothesis.

If I have correctly interpreted Hoshino's observations, flowering time in peas is clearly a Mendelian unit-character, entirely devoid of dominance, so that a strictly intermediate hybrid form is the commonest end-product of a single cross between early and late varieties. Further, segregation is imperfect so that blending results, which becomes more and more complete with each generation of inbreeding. From the incompleteness of the blending in the F_1 zygote and so the imperfection of the segregation in the F_1 gametes, it follows that many different types of F_2 zygotes are produced, some of which are practically constant (homozygous) particularly those at either extreme of the series (the "early constant," "pseudo-early constant," "late constant" and "pseudo-late constant") and also at two intermediate points ("intermediate early" and "intermediate late").

Other F_2 zygotes, resulting from the union of gametes quite dissimilar, produce a highly variable F_3 progeny, but one which will give rise to F_4 families individually less variable for two reasons: (1) because the process of blending continues and so gametes produced by the same zygote become more like each other than were the parent gametes of that zygote, and (2) because heterozygotes under self-fertilization tend to produce about 50 per cent. of homozygous offspring, while homozygotes produce only homozygous offspring.

The entire population therefore will in accordance with recognized Mendelian principles gradually resolve itself into relatively constant self-fertilizing lines. But because of the slow but continuous blending which occurs, these pure lines will in a very few generations form a complete gradation of forms connecting one parental mode with the other. The most numerous of these intermediate forms will in F_4 and later generations be that which is midway between the modes of the respective parents.

This case throws a flood of light on the nature of blending and of Mendelian inheritance and of their relations to each other. In typical Mendelian inheritance determiners of allelomorphic characters may meet each other generation after generation in a common zygote, separating again in gametogenesis without apparent modification of either in consequence of their conjugation in a heterozygote. This is well illustrated in the color inheritance of animals and plants.

In typical blending inheritance the determiners of contrasted parental conditions apparently blend into a determiner of intermediate character, the gametes formed by an F_1 individual being practically as uniform in character as those of either parent individual. Blending is illustrated in the inheritance of ordinary size differences in birds and mammals (Castle, 1916).

A third type of inheritance must now be recognized which is a compromise between these two, for it exhibits Mendelian segregation of the contrasted parental conditions but with modification due to partial blending of the unlike determiners in the F_1 zygote. The blending increases and evidences of segregation decrease with every generation during which the contrasted characters remain in conjugation. Consequently with every generation of inbreeding or self-fertilization following a cross of this sort, a stable intermediate class is more and more closely approached until its realization is complete. See Marshall (1916) on the Corriedale breed of sheep. The existence of this third type of inheritance was pointed out by Castle and Forbes (1906) in the case of hair-length in guinea-pigs and by Castle (1906) in the case of polydactylism in guinea-pigs. The opinion was then expressed that "more characters fall in this category than in any other." Hoshino's observations on flowering time in peas (if I rightly interpret them) fully establish the existence of this third type of inheritance. Incidentally they indicate that the Nilsson-Ehle principle of multiple determiners to explain blending inheritance is quite superfluous.

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